Records of the Western Australian Museum 18: 263–276 (1997).

A new species of pliosaurid reptile from the Early Cretaceous Birdrong Sandstone of Western Australia

Arthur R. I. Cruickshank [1] and John A. Long [2]

[1] Earth Sciences Section, Leicestershire Museums, Arts and Records Service, The Rowans, College Street, Leicester LE2 0JJ, U.K.

[2] Department of Earth and Planetary Sciences, Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia

Abstract – Of three partial skeletons of small pliosauroid plesiosaurs from near Kalbarri in the Carnarvon Basin, Western Australia, two are described as *Leptocleidus clemai* sp. nov. The third is indeterminate. These constitute the first associated partial skeletons of Mesozoic reptiles recovered from Western Australia, and the first named species of fossil reptile from the State (excluding footprint inchnotaxa). They came from the (upper) glauconitic facies of the Birdrong Sandstone, a late Hauterivian-Barremian (Early Cretaceous) transgressive unit representing a nearshore shallow-marine episode of deposition. Fossil wood associated with the pliosaurs contains fossil pholadid bivalve borings and hyphae of saprophytic fungi. *Leptocleidus* is a small-sized (ca 3 m) genus of pliosauroid plesiosaur which is known from 'Wealden' deposits in England, South Africa and Australia. It retains many characters seen in *Rhomaleosaurus*, a pliosauroid of the English Lias (Hettangian -Toarcian; Early Jurassic). The new species *Leptocleidus clemai* sp. nov. is characterised by being the largest of the known species. Characters of the genus *Leptocleidus* are discussed. A brief review of the distribution of pliosauroids in time shows that the large, open-water, sarcophagous forms appear to have died out at the end of the Turonian and are replaced by the mosasaurs which first appear in the Cenomanian. *Leptocleidus*-like forms seem to have been restricted to inshore habitats.

INTRODUCTION

Pliosauroid plesiosaurs are a characteristic component of many marine faunas throughout the Mesozoic (Brown 1981; Taylor 1992; Cruickshank 1994, 1996a). They represent the top predators of the time and grew to over 14 m in length (*Kronosaurus*, Albian of Queensland). The contrasting plesiosauroids could also grow to extreme lengths, but they were not adapted for the role of sarcophagous predators, being instead pursuers of soft-bodied, or lightly armoured, small prey species (Brown 1981; Massare 1987; Cruickshank and Fordyce, in prep.). The morphological contrast between the superfamilies Pliosauroidea and Plesiosauroidea involves differences in the relative size of their heads, and length of their necks; pliosaurs having relatively large heads and short necks (Tarlo 1960; Taylor 1992; Cruickshank 1994). The morphology of the body and limbs seems not to have varied significantly between plesiosaur and pliosaur, and they all adopted a form of underwater flight as their main form of propulsion (Storrs 1993; Riess and Frey 1991).

Evolutionary trends in the Plesiosauria have been well documented by Brown (1981), and within the Pliosauroidea there is a conventional view of a general increase in body size through time, a relative increase in head length at the expense of neck length, and an overall decrease in both the number of neck vertebrae and the length of individual centra (Brown 1981; Tarlo 1960). However *Leptocleidus*-like pliosauroids seem not to follow these trends, and keep a neck vertebral count of near 30, do not reduce the lengths of the centra, and have a small body size (ca 3 m). Much of their anatomy is very close to that of the genus *Rhomaleosaurus*, the 5.0 m long top predator of the European Lias (Early Jurassic) (Taylor 1992; Cruickshank, 1996a).

Plesiosaurians have been known from Australia for a number of years (Molnar 1991), but the record in Western Australia is not so complete (e.g., Teichert and Matheson 1944; Long 1993) and the material reported here adds significantly to the knowledge of distribution of these animals in the Australian Cretaceous. Over several collecting expeditions from late 1992 to 1994, sponsored by Mr John Clema and Forrestania Gold Pty Ltd, the remains of three pliosauroid plesiosaurs were

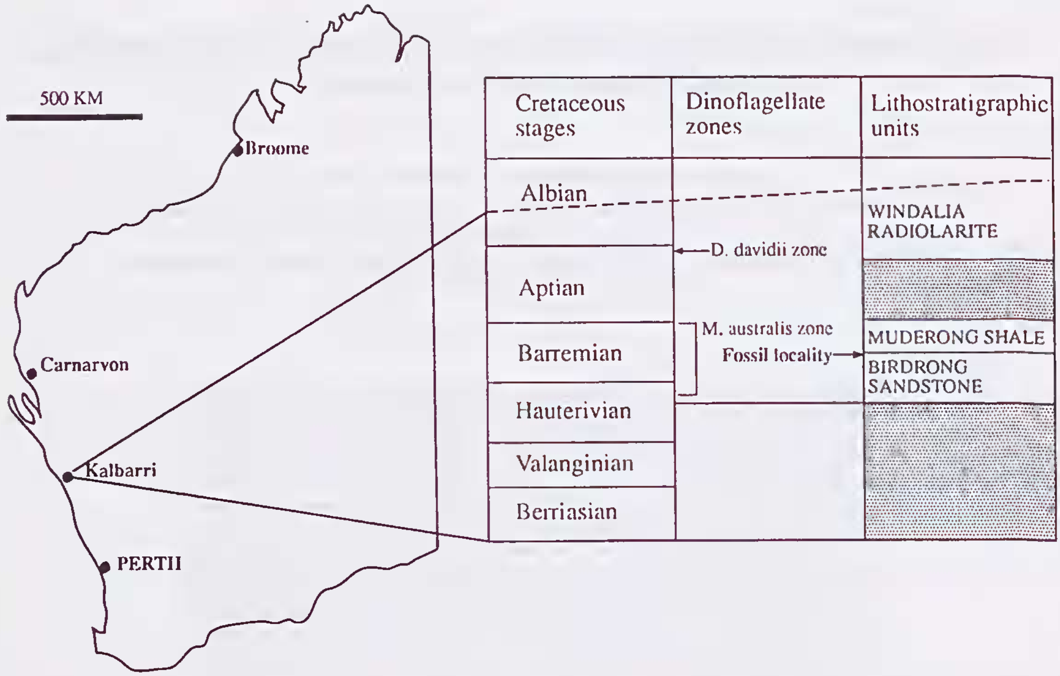


Figure 1 Locality and stratigraphic setting of the pliosaurs from near Kalbarri, Carnarvon Basin, Western Australia. Scale bar =500 km

recovered from the Birdrong Sandstone outcrop near Kalbarri in the Carnarvon Basin, Western Australia and isolated sauropterygian remains were also recovered from outcrops in the northern Carnarvon Basin, near Coral Bay (McLoughlin *et al.* 1995; Hocking *et al.* 1987) (Figure 1). The skeletons all lack skull material, but are well enough preserved to be ascribed to a new species of the 'Wealden' (Early Cretaceous) genus *Leptocleidus* Andrews 1922 on size differences of their postcranial bones. This genus is known from England and South Africa (Andrews 1911; 1922; Cruickshank 1997), and probably from the Albian/ Aptian of Coober Pedy, Australia (Schroeder in prep.), although the new species described herein becomes the first species of the genus to be formally named ed from Australia.

Incorporated in the material described below are a few anomalous bones which do not seem to be part of plesiosaurian skeletons. One (found near the specimen may be a mid-caudal vertebra from a theropod dinosaur, and three others, from another skeleton (WAM 92.8.1) could possibly be from a jaw too big to belong to a pliosaur of the presumed size of the species described here. The purpose of this paper is put these discoveries on record, pending a fuller review of other *Leptocleidus* occurrences in the Early Cretaceous.

The Birdrong Sandstone

In the Carnarvon Basin the Cretaceous rocks generally lie on an erosion surface cut into Permian strata (Figure 1), although in Kalbarri the Cretaceous sequence rests unconformably above the ?Silurian Tumblagooda Sandstone. The Birdrong Sandstone is the basal unit and is ca 10 m thick, being overlain by 56 m of the Muderong Shale, a carbonaceous mudstone-siltstone. The Birdrong Sandstone belongs to the *Muderongia australis* Zone of late Hauterivian-Barremian age, as does the lower part of the Muderong Shale (McLaughlin *et al.* 1994). The age of the upper Muderong Shale is uncertain, as is the age of the 10 m thick sandstone unit which separates the Muderong Shale from the late Aptian Windalia Radiolite. Changes in sediment composition, palynomorph assemblages and forminiferal biofacies reflect retrogradation of marine facies during deposition of the Birdrong Sandstone and lowermost Muderong Shale, followed by aggradation through most of the Muderong Shale, with a maximum water depth of never more than 50 m. At its type section on Mardathuna Station, northeast of Carnarvon, the Birdrong Sandstone begins with a fluviatile phase of deposition, followed by deltaic and shallow marine facies (Hocking *et al.* 1987).

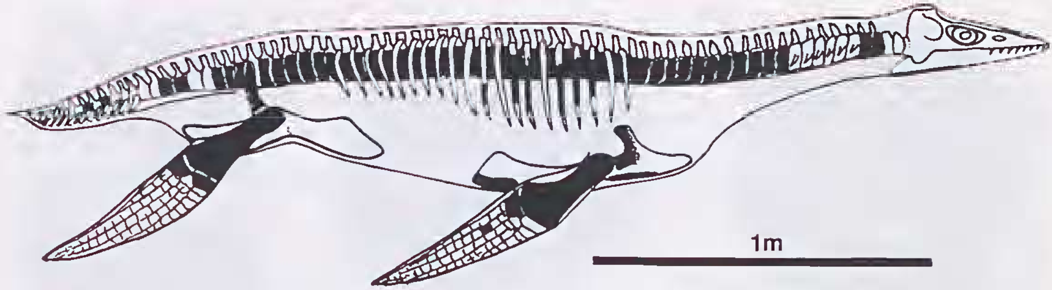


Figure 2 Attempted reconstruction of the skeleton of *Leptocleidus clemai* sp. nov. showing relative completeness of remains so far recovered shown in black. Skull and other proportions are based on *Peloneustes* and *Leptocleidus* sp.

The sequence reflects a transgressive pulse that was part of the progressive submergence of vast areas of the Australian continent during the Early Cretaceous (Dettmann *et. al.* 1992). This late Hauterivian-Barremian transgressive pulse is recognized in widely separated basins in Australia, and may represent a synchronous continent-wide sea-level rise. A similar sea-level rise is seen in the Algoa Basin (and other smaller basins) on the South African south-east coast, where *Leptocleidus capensis* has been recovered from Valanginian inshore deposits (Cruickshank 1997; McLachlan and McMillan 1977; McMillan in prep.). The earlier date for the South African deposits reflects a probable earlier phase of the break-up of (east) Gondwana.

Institutional abbreviations used in this paper: WAM – fossil collections of the Department of Earth and Planetary Sciences; SAM – fossil collections in the Division of Palaeontology, South African Museum; NHM – fossil collections in the Palaeontology Department, The Natural History Museum, London.

MATERIAL AND METHODS

(a) WAM 92.8.1–1 to 68. The first specimen to be recovered comprises numerous vertebral centra, left and right femora, right tibia and fibula, left tibia, a possible partial ulna, base and part of the shaft of a left ilium, a badly damaged head of a humerus, broken parts of the pectoral girdle (scapula?) and pelvic girdle elements, part of a neural arch, and several rib fragments. The centra are distributed as follows: 11 cervical, 3 pectorals, 17 dorsal, 2 sacrals(?), 5 caudals and one so badly preserved that its position is not identifiable, but it is possibly a dorsal. In addition to the elements which can be confidently assigned to a pliosaur, there are three heavily ossified portions of what appear to be the mid-part of a lower jaw, lacking teeth, which if reconstructed would be far too big for the assumed size of this pliosaur.

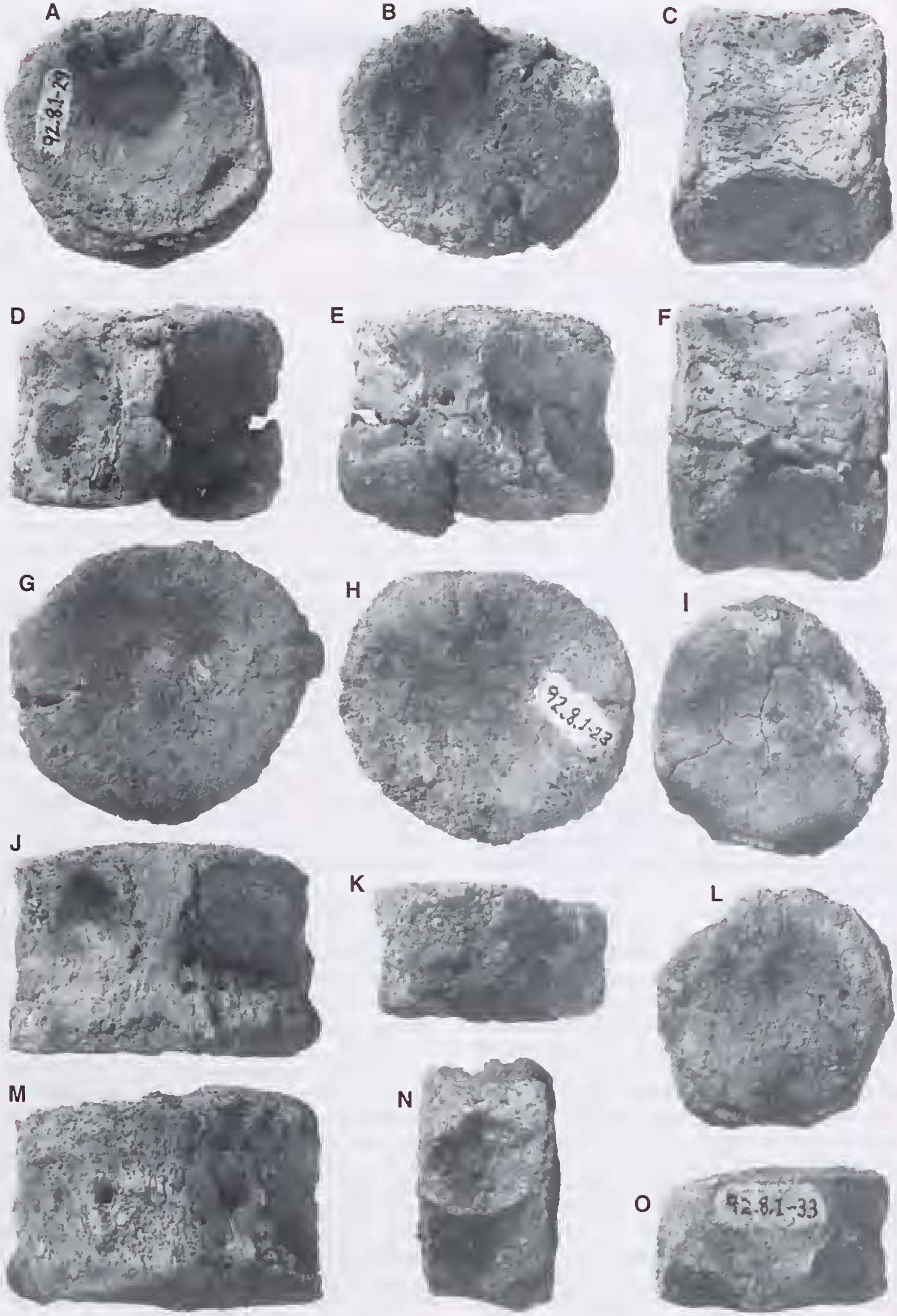
(b) WAM 94.1.6–1 to 100. The second best preserved of the three. It comprises a length of the vertebral column encased in a nodule extending over about 15 vertebrae, and the following individual bones which can be identified: 9 cervical vertebrae, about 20 dorsal vertebrae as well as some fragments, 4 sacrals, one caudal, a fragment of scapula, portions of two ilia and, a piece of pubis, two humeri, one possible phalanx, an unidentifiable epipodial and five pieces of rib, apart from some very poorly preserved lengths of rib still in the nodule.

A very badly preserved, but elongate, centrum found near the specimen is not plesiosaurian but is from the mid-caudal region of a medium-sized theropod dinosaur, and is described elsewhere (Long and Cruickshank 1997).

(c) WAM 96.5.2. The material comprising this specimen is badly preserved and mostly unidentifiable as to taxon, except for some dorsal vertebrae which appear to be similar in size and proportion to those of the other two specimens. It is noted here only to complete the record.

Figure 2 shows a generalised pliosaurid skeleton with the known remains from *Leptocleidus clemai* sp. nov. shaded in black, indicating the degree of completeness from the combined two partial skeletons.

Excavation and preparation procedures used on this material were standard, using pneumatic airscribes and manual chisels to clear the friable sandy matrix and the thin layer of encrusting iron-rich cementing minerals from the specimens. Mends were made with proprietary organic glues dissolved in acetone, and therefore reversible, except for the joining together of the thicker bones (eg the humeri) in which epoxy resins were used. Some portions of the specimens were transported in plaster jackets and extracted from the matrix in the laboratory. Measurements were made to the nearest 0.1 mm, using sliding vernier calipers.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
92.8.1-29
92.8.1-23
92.8.1-33

SYSTEMATIC PALAEONTOLOGY

Class Reptilia

Subclass Sauropterygia Owen, 1860

Order Plesiosauria de Blainville, 1835

Superfamily Pliosauroidea (Gray, 1825) Welles, 1943

Family Pliosauridae Seeley, 1874

Genus *Leptocleidus* Andrews, 1922

Type species

Leptocleidus superstes Andrews, 1922

Emended diagnosis

Leptocleidus can be defined as a small genus of pliosauroid possessing cranial and postcranial characters of a conservative kind, being in many ways no more derived than the Liassic (Early Jurassic) genera *Eurycleidus* and *Rhomaleosaurus* (Andrews 1922; Cruickshank 1994, 1996a; Taylor 1992). Skull triangular in outline, with a prominent midnasal ridge which merges with the parasagittal crest, flanked by deep grooves or depressions which in turn cause the orbital rims to stand up from the general profile of the skull. Compared with *Rhomaleosaurus* the tooth count is reduced, to 21 positions on each side of the upper jaw (5 in each premaxilla + 16 in each maxilla), compared with at least 27 in the upper jaw of *R. megacephalus* (Cruickshank 1994), and a similar number in *R. zetlandicus* (Taylor 1992; Cruickshank 1996a). No complete jaw is known for the genus, but an estimated tooth count is 35 *(L. capensis)*, at the lower end of the known range for pliosaurids. A spatulate lower jaw symphysis with five pairs of teeth is assumed for *L.capensis* (Cruickshank 1997). *Leptocleidus* possesses a dorsomedially directed trough on the prearticular and adjacent bones of the lower jaw, similar to *Rhomaleosaurus*. Pectoral girdle primitive, having large clavicles and interclavicles and small scapulae (Andrews 1922); humerus has a very much more symmetrical (fan-shaped) distal end, in contrast to *Rhomaleosaurus* which has the humerus gently curved posteriorly (Cruickshank 1996a; in press). None of the vertebrae are compressed, cervicals being spool-shaped with the neural arches relatively large when compared with, for example, *Pliosaurus brachyspondylus* (Taylor and Cruickshank 1993). Cervical vertebral count in excess of 13. *Leptocleidus* differs from early forms in one other feature in possessing a forwardly-pointing expansion ('cockscomb') on the squamosal mid-line, at the rear of the parasagittal crest, very similar to that seen in Late Cretaceous Polycotylidae (Welles 1962; Thurmond 1968).

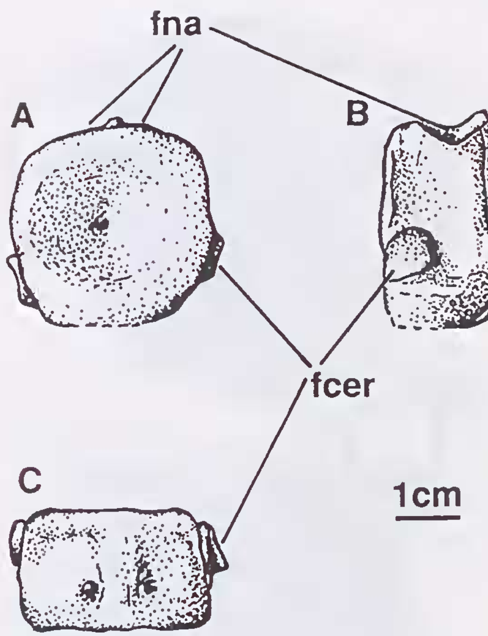


Figure 4 *Leptocleidus clemai* sp. nov. Anterior cervical vertebra of WAM 94.1.6– 64, in anterior (A), left lateral (B) and ventral (C) views. Scale bar = 1 cm. Abbreviations: fna, fossa for neural arch; fcer, attachment of cervical rib.

Remarks

The genus has been redefined in the light of new material plus observations of undescribed specimens made by one of us (ARIC). We consider it important to include this here as further new specimens of the genus have been uncovered throughout eastern Australia which we anticipate will be described in the near future. It should be noted that jaw morphology and possibly the humerus and cervical vertebral morphology and count follow closely those of Early Jurassic genera such as *Rhomaleosaurus*. This is unusual in that it is usually recognised that by the Late Jurassic pliosaurs reduced their neck vertebral count to 13 highly compressed disc-like centra. The presence

Figure 3 *Leptocleidus clemai* sp. nov. Holotype 92.8.1. A–E, cervical vertebra 92.8.1–29, seen in anterior (A), posterior (B), left lateral (C), dorsal (D) and ventral (E) views. F–H, J, M, postcervical vertebra, 92.8.1–23 in left lateral (F), anterior (G), posterior (H), dorsal (J) and ventral (M) views. I, K,L,N,O, caudal vertebra 92.8.1–33 in posterior (I), dorsal (K), anterior (L), left lateral (N) and ventral (O) views. All shown natural size.

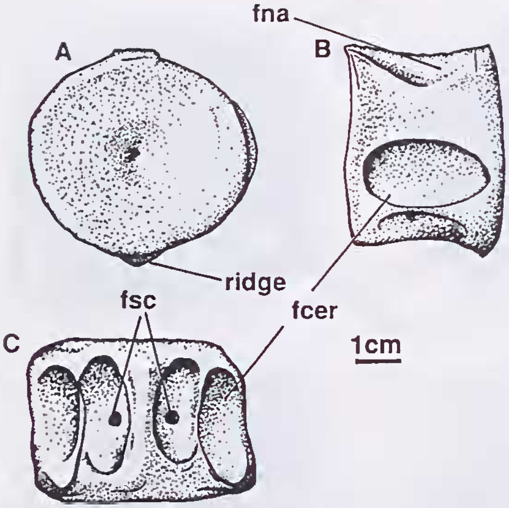


Figure 5 *Leptocleidus clemai* sp. nov. Mid cervical vertebra of WAM 92.6.1–30 in anterior (A), lateral (B) and ventral (C) views. Scale bar = 1 cm. Abbreviations: fna, fossa for neural arch; fcer, attachment of cervical rib; fsc, subcentral foramina.

of a dorsomedian trough on the inner surface of the articular region of the lower jaw was thought to be an autapomorphy of *Rhomaleosaurus* (European Lias).

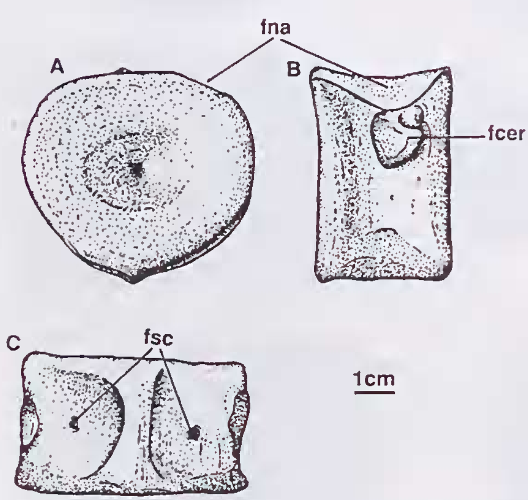


Figure 6 *Leptocleidus clemai* sp. nov. Posterior cervical vertebra of WAM 92.8.1–20 in anterior (A), lateral (B) and ventral (C) views. Scale bar = 1 cm. Abbreviations as for Figure 5.

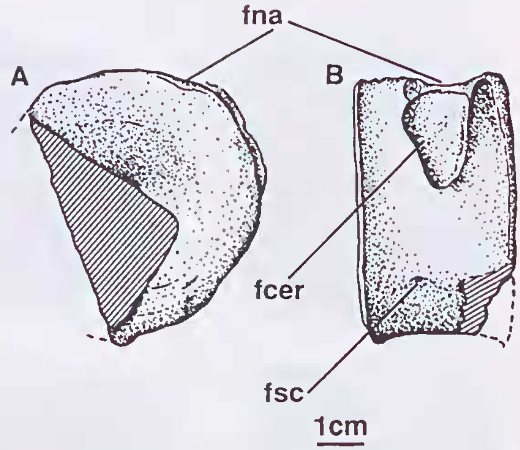


Figure 7 *Leptocleidus clemai* sp. nov. Posterior cervical vertebra of WAM 94.1.6 – 60 in anterior (A) and lateral (B) views. Scale bar = 1 cm. Abbreviations as for Figure 5.

Leptocleidus clemai sp. nov.
Figures 3–16

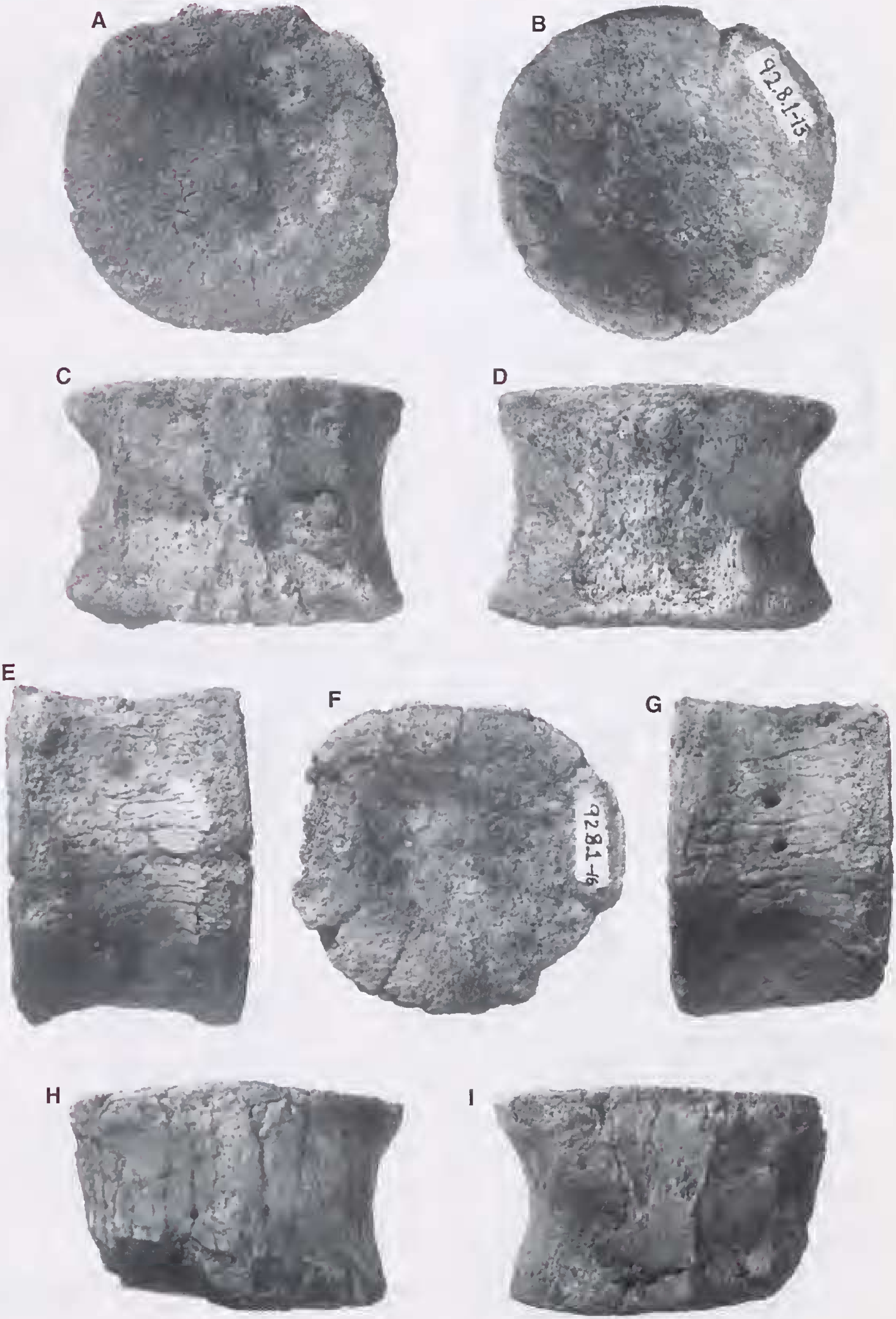
Type specimen

Holotype is WAM 92.8.1–1 to 68 (Figs. 3, 5,6, 8–12, 13A, C–E,14, 16), a partial skeleton comprising right femur (92.8.1–2), part of tibia (92.8.1–3), parts of the left femur (92.8.1–4), possible fragments of lower jaw, lacking teeth, (92.8.1–5A, B), pelvic girdle element (92.8.1–7), part of a propodial head (92.8.1–8), part of left ilium (92.8.1–9), portion of ilium shaft (92.8.1–56), lower jaw? fragment (92.8.1–57), ?part of scapula (92.8.1–58), various bone fragments and parts of neural arches (92.8.1–59 to 92.8.1–64), left ulna (92.8.1–65), right ulna (92.8.1–66), right radius(92.8.1–67) part of propodial? (92.8.1–68) and some 45 vertebrae (92.8.1–10 to 92.8.1–55). All specimens of *Leptocleidus clemai* sp. nov. are housed in the palaeontological collections of the Western Australian Museum.

Horizon and locality

The exact localities have been kept private at a request from the property manager, but they are recorded in the Department of Earth and Planetary Sciences locality register (within the Western Australian Museum). Upper metre of the Birdrong Sandstone, Early Cretaceous (Hauterivian-Barremian), Kalbarri region, Western Australia.

Figure 8 *Leptocleidus clemai* sp. nov., WAM 92.8.1, dorsal vertebrae. A–E, 92.8.1–13 in posterior (A), anterior (B), dorsal (C), ventral (D) and right lateral (E) views. F–I, 92.8.1–16 in anterior (F), left lateral (G). ventral (H) and dorsal (I) views. All shown natural size.


A
B
92.8.1-15
C
D
E
F
92.8.1-16
G
H
I

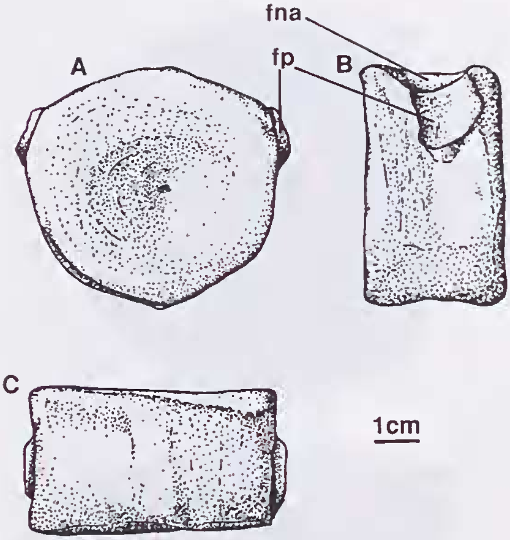


Figure 9 *Leptocleidus clemai* sp. nov. First pectoral vertebra of WAM 92.6.1–21 in anterior (A), left lateral (B) and ventral (C) views. Scale bar =1 cm. Abbreviations: fna, fossa for neural arch; fp, pectoral rib attachment.

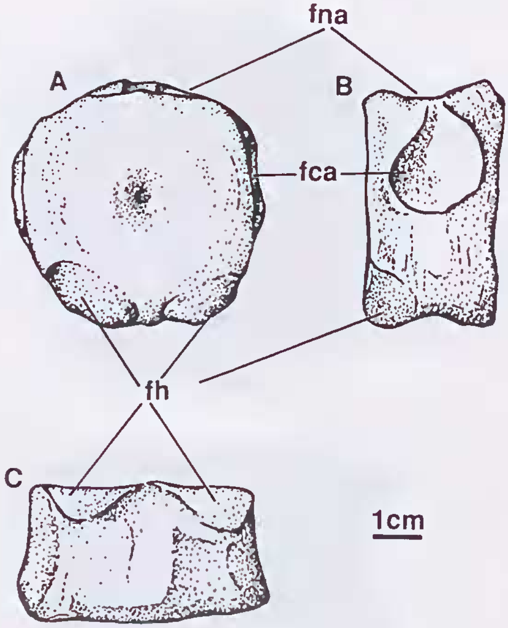


Figure 11 *Leptocleidus clemai* sp. nov. Caudal vertebra of WAM 92.8.1–54 in anterior (A), left lateral (B) and ventral (C) views. Scale bar =1 cm. Abbreviations: fca, fossae for transverse ribs, fh, fossae for attachment of chevron bones, fna, fossae for neural arch attachment.

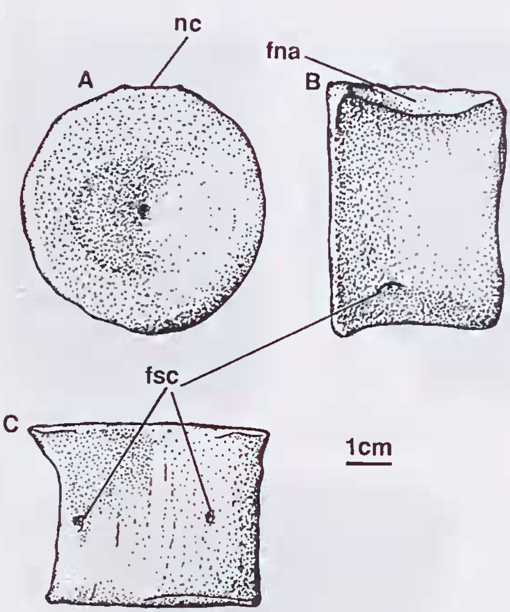


Figure 10 *Leptocleidus clemai* sp. nov. Dorsal vertebra of WAM 92.8.1–14 in anterior (A), left lateral (B) and ventral (C) views. Scale bar =1 cm. Abbreviations. fna, fossa for neural arch; fsc, sub-central foramina; nc, fossa for neural cord.

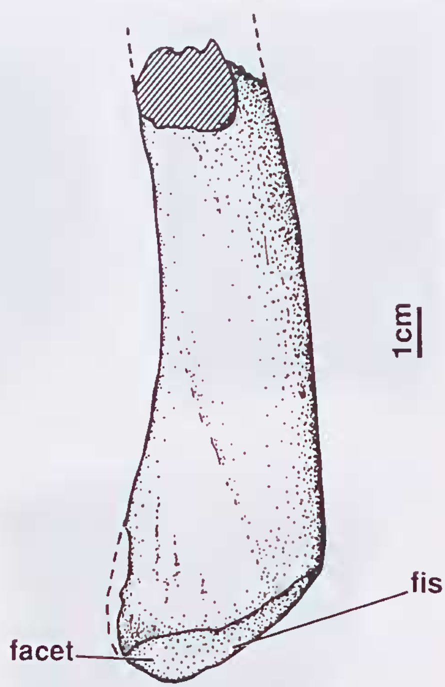


Figure 12 *Leptocleidus clemai* sp. nov. Left ilium of WAM 92.8.1–9. Scale bar = 1 cm. Abbreviations: fis, median fissure of ilia.

Referred material

WAM 94.1.6–1 to 100 (94.1.6–1 through to 94.1.6–94), a less well preserved partial skeleton, dimensionally very similar, approximately 100 associated, partially articulated bones found underneath a single large concretion (Figures 4, 7, 13B, 15).

Etymology

In honour of Mr John M. Clema of Perth, Western Australia, who has generously supported and assisted in fossil collecting expeditions by the Western Australian Museum over the years 1993–1995.

Diagnosis

A species of *Leptocleidus* whose vertebrae are at least 30% greater in linear dimensions than those of either *L. superstes* or *L. capensis*, and whose propodials are 10% – 15% greater in size (WAM 92.8.1–2, femur 274 mm long). The epipodials show a derived state when compared with *L. capensis* in being wider than long.

Description of material

Holotype (WAM 92.8.1, Figs. 3, 5,6, 8–12, 13A, C–E,14, 16).

Distinguishing between the various parts of the vertebral column was difficult in both the principal specimens reported here due to the poor state of preservation and fracturing of vertebrae. It has been assumed that the distinction between cervical and sacral centra is that the former have a mid-ventral keel, and prominent sub-central foramina in addition to the facets for the cervical ribs, which possibly could be confused with one or other of the sacral series. Pectoral centra do not have the prominent mid-ventral keel, but the most anterior pectoral centrum has a large part of its rib facet still on the centrum, which in a poorly preserved specimen also might cause confusion with one of the sacral series. Caudal centra, apart from the very first few, have haemal facets and should not be confused with any others. Dorsal centra do not have rib facets and often do not have prominent sub-central foramina nor mid-ventral keels. They are often very much more robust than others in the vertebral column.

All the centra are spool-shaped (Figures 3–11), are concave on their faces, and none has its neural arch in position. Mostly the evidence points to the bases of the neural arches having come cleanly away from the centra, indicating lack of fusion and hence a sub-adult ('juvenile') age for the specimen. The centrum with the greatest length is a dorsal at about 42.4 mm. The shortest is a caudal at 22.5 mm. All centrum widths are significantly greater than their lengths, and also greater than, or sub-equal to their heights. The cervical vertebrae are not markedly shortened (Figures 3A–E). They are only slightly shorter than the pectorals, but more so when compared with the dorsals (Table 1). However the overall impression is a vertebral column of uniformly proportioned centra, as far back as the caudal series, when some compression is seen. This is a markedly primitive vertebral column for a Cretaceous pliosaur (Andrews 1922; Brown 1981; Tarlo 1960; Taylor and Cruickshank 1993), but seems to be very similar to the other species of *Leptocleidus* (*L. capensis* (Andrews 1911) and *L. superstes* Andrews 1922), differing only in the overall size of the individual elements.

Of the femora, the right is best preserved (Figs 13A, 14). Its dimensions are 274.0 mm long, 76.3 mm across the head and 123.4 mm wide distally.

Table 1 Some measurements of *Leptocleidus* specimens. The vertebral measurements are listed in sequence as 'Length', 'Breadth' (Width) and 'Height'. The limb bone measurements are overall length, width of head in plane of the distal expansion, and width of distal end.

Identity	*L. superstes* BMNH R4824	*L. capensis* SAM K–5822	*L. clemai* WAM 92.8.1	*L. clemai* WAM 94.1.6
post cervical	25 38 30	19 30 35	35.4 63.3 55.2	39.4 56 55.5
ant cervical	22 25 25			20 34.2 30.7
mid cervical		25 36 31	35 48.9 44.6	
post cervical	25 38 30	19 30 35	35.4 63.3 55.2	39.4 56 55.5
	32 43 40	21 33 27	35.6 62.3 54.7	
dorsal	31 55 48	32 50 41	40.5 52.6 52.1	32.5 55.8 49.5
		28 46 41	40 60.9 58.3	35 58 53.5
			41.9 63.9 64.1	41.2 73.1 68
l.humerus	245 60 124			
r.humerus				270 68.2 127.6
r.femur			274 76.3 123.4	

Figure 13 *Leptocleidus clemai* sp. nov., A, femur in dorsal view, WAM 92.8.1–2, x0.5. B, lower part of left ilium, 92.8.1–9, x1. C, humerus in dorsal view, WAM 94.1.6–95, x0.5. D, tibia, 92.8.1–66 in dorsal view, x1; E, fibula, 92.8.1–67, in dorsal view, x1.

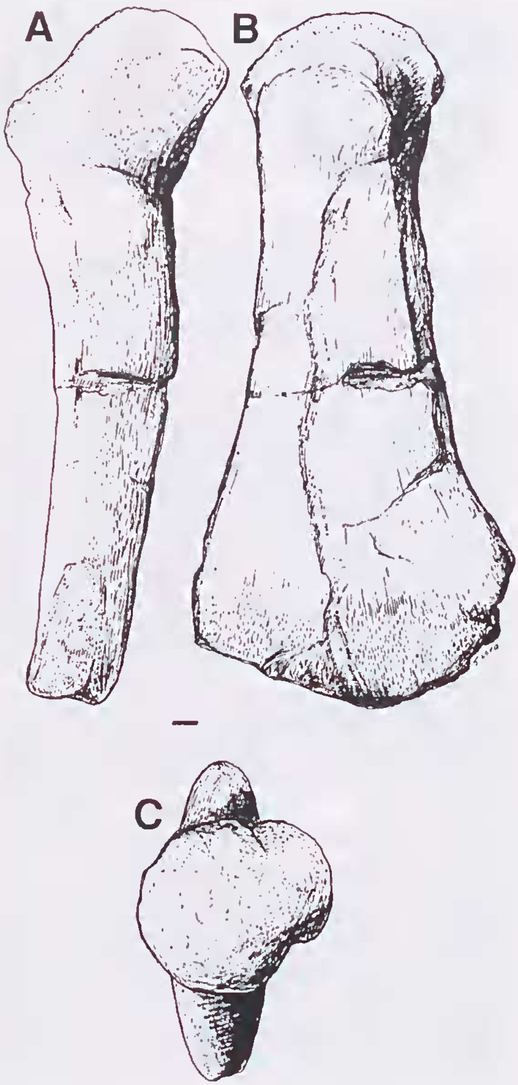


Figure 14 *Leptocleidus clemai* sp. nov., WAM 92.8.1–2, femur, in anterior (A), dorsal (B) and proximal (C) views.

There is a notch developed betwen the tibia and fibula, which are wider than long (Figure 16). The ilium (Figures 12, 13C) is well ossified, but its distal end is not preserved.

WAM 94.1.6–1 to 100 (Figs 4, 7, 13C, 14)

The second specimen seems to be identical with the foregoing, so little of the corresponding material is illustrated. The vertebrae range in overall length from 20.0 mm for an anterior cervical (Figure 4) to 41.2 mm for a dorsal centrum (Figure 11). Sacral vertebrae range from 28.0 mm to 38.2 mm, and cervicals range in length up to 39.7 mm. These sizes coincide with those for WAM 92.8.1 with the exception of the anterior cervical vertebra, which is from a region of the neck much further forward than in WAM 92.8.1.

The complete right humerus of WAM 94.1.6 (Figures 13C, 15) is 270 mm long, 68.2 mm across the head and 127.4 mm across the distal expansion (Table 1). It does not have the preaxial expansion seen in other late pliosaurs, and is reminiscent of the humeri of Early Jurassic plesiosaurs (Cruickshank 1996b).

These specimens represent two sub-adult small pliosaurids with an estimated maximum length of 2.5 to 3 m. (based on proportions of *Rhomaleosaurus*), from shallow marine waters of the Early Cretaceous of Western Australia, which vary from other known members of the genus *Leptocleidus* only in their greater size.

DISCUSSION

Maturity of specimens

A question as to whether the specimens described here are juvenile or not deserves comment. The limb bones are all very well ossified and do not give the impression of being from young animals. However the neural arches of the two other species of *Leptocleidus* are firmly fused to their centra, and certainly these two specimens must be regarded as 'adult'. Notwithstanding these observations, the specimen of *Pliosaurus brachyspondylus* described by Taylor and Cruickshank (1993) is a very large animal (skull length ca 2m), the skull sutures were well fused, and yet the cervical vertebrae did not have their neural arches fused. It is unlikely that an observer would have called that animal, if seen alive, "juvenile'. We prefer to regard these specimens from the Birdrong Sandstone as being sub-adult, probably being close to fully grown when they died.

Distribution of 'primitive' pliosauroids

Leptocleidids (Early Cretaceous) seem to be very similar to, if smaller than, rhomaleosaurid (Early Jurassic) pliosaurs. An ancestor-descendant relationship can be confidently inferred for them (Cruickshank 1996a). They seem to have been inhabitants of the close-inshore, marine, environments in a manner similar to modern sea-lions, and may have moved to this environment under pressure from the later, larger, Jurassic forms such as *Liopleurodon*, *Simolestes*, *Pliosaurus* and *Peloneustes* (Andrews 1910 – 1913; Taylor and Cruickshank 1993). These large forms, in the Cretaceous, are typified by the genus *Kronosaurus*, but which did not survive beyond the Turonian,

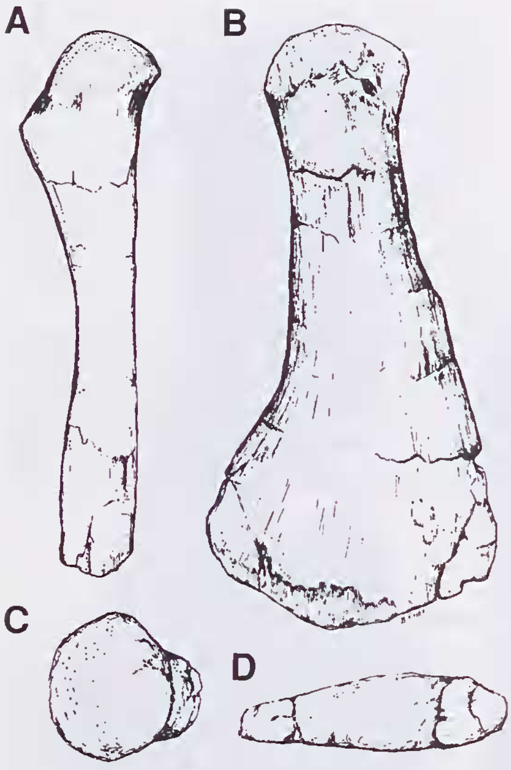


Figure 15 *Leptocleidus clemai* sp. nov., WAM 94.1.6–95, humerus in anterior (A), dorsal (B), proximal (C) and distal (D) views.

leaving only the polycotylid pliosaurs as the last remaining representatives of the Pliosauroidea (Benton 1993). It is worth noting in this respect that the first mosasaurs are known from the

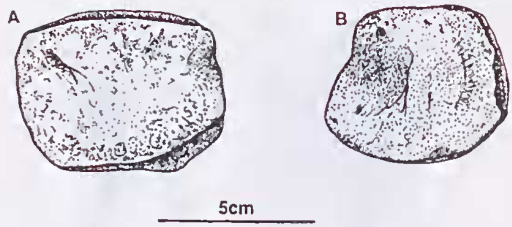


Figure 16 *Leptocleidus clemai* sp. nov. A, WAM 92.8.1–66, right tibia in dorsal view. B, WAM 92.6.1–67, right fibula of in dorsal view. Scale bar = 1 cm.

Cenomanian, about the same time as ichthyosaurs become extinct worldwide (Benton 1993), and may have been able to out-compete the pliosaurs in some way not yet known. Maybe they were the more capable swimmers (Massare 1988). They certainly had a very different feeding mechanism. But the puzzle is, if the large pliosaurids disappeared, then why not the cryptoclidids and elasmosaurs? Both of these families survived right to the end of Cretaceous times (Cruickshank and Fordyce in prep.).

Leptocleidids are known to occur in association with other shallow marine to fluvial vertebrate assemblages. In the English Wealden, a lagoonal deposit, remains of *L.superstes* occur with terrestrial dinosaurs (e.g., *Hypsilophodon*, *Iguanodon*, *Baryonyx*). In South Africa *L. capensis* occurs in an inshore marine to lagoonal deposit whose foraminifera have a heavy nonmarine imprint, and remains of terrestrial dinosaurs and wood also occur in close association. In South Australia the Early Cretaceous deposits of Coober Pedy and Andamooka containing *Leptocleidus* sp. (the famous "Eric" specimen at the Australian Museum, Sydney) also yield the remains of terrestrial

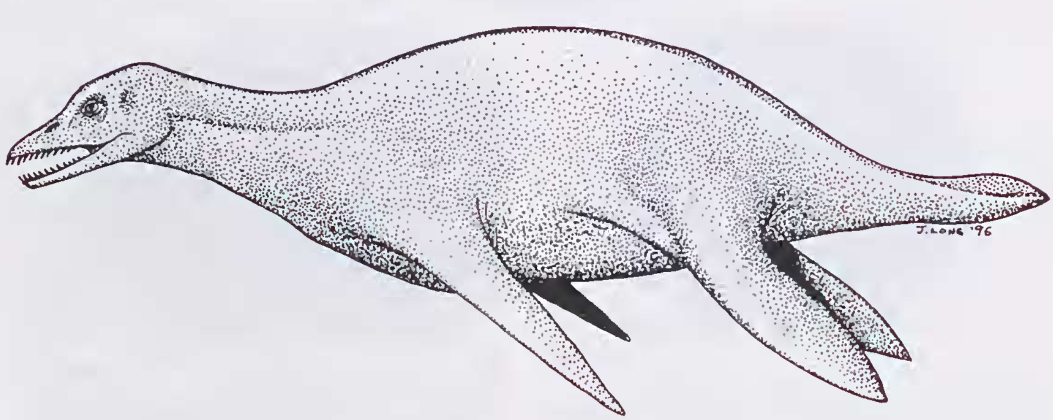


Figure 17 Attempted reconstruction of *Leptocleidus clemai* sp. nov. by J.Long.

dinosaurs (e.g., *Kukuru kujani* Long 1993) together with fossilised wood. Thus the noted occurrence of a theropod dinosaur bone found near WAM 986.8.1 along with the high abundance of fossilised wood from the Birdrong Sandstone strongly suggests that this unit would be a potentially good target to direct future exploration for dinosaurs.

SUMMARY AND CONCLUSIONS

Two partial skeletons from the Early Cretaceous Birdrong Sandstone of Western Australia are ascribed to the pliosauroid genus *Leptocleidus* as *L. clemai* sp.nov. *Leptocleidus* is a small-sized genus (under 4 m), known from the Early Cretaceous of England, South Africa and Australia. It seems to have occupied a close inshore or shallow marine habitat, as opposed to the more typical open marine habitat of the larger forms such as *Kronosaurus*. *Leptocleidus* is close to, but smaller than, the Early Jurassic genus *Rhomaleosaurus*. It may be ancestral to the later Cretaceous forms known as the Polycotylidae. It is noted that the large pliosaurids died out by the Turonian and were replaced by the mosasaurs, leaving the polycotylids as the last remaining pliosaurs. An anomaly is that the plesiosauroid plesiosaurs continued very successfully as predators on small and soft-bodied marine animals until the end of the Mesozoic.

ACKNOWLEDGEMENTS

We thank the generous sponsorship of Mr John Clema, of Forrestfield, and Forrestania Gold Pty Ltd, for grants fully supporting field exploration of the Birdrong Sandstone over three field seasons (1992–1994), and partial funding of preparation of specimens. Many helpers assisted in the field excavations or offered helpful discussion of the age of the sites, so we extend our sincere thanks to Greg Milnar, Ian Copp and Glynn Ellis, Kristine Brimmell, David Haig, Alex Ritchie, Mikael Siverson, Alex Baynes and John Clema. We thank Kristine Brimmell for the photography of the specimens, Jenny Bevan for preparation of specimens, and Danielle Hendricks for drafting assistance. ARIC is indebted to the Royal Society of London for travel support, and to the three women in his life for encouragement and help in undertaking a long research visit to the antipodes in early 1996.

REFERENCES

Andrews, C.W. (1910–1913). *A descriptive catalogue of the marine reptiles of the Oxford Clay*. Parts 1 & 2. British Museum (Natural History), London.

Andrews, C.W. (1911). Description of a new plesiosaur (*Plesiosaurus capensis*, sp.nov.) from the Uitenhage Beds of Cape Colony. *Annals of the South African Museum* **1**: 309–322.

Andrews, C.W. (1922). Description of a new plesiosaur from the Weald Clay of Berwick (Sussex). *Quarterly Journal of the Geological Society of London* **78**: 285–298.

Brown, D.S. (1981). The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the Plesiosauria. *Bulletin of the British Museum (Natural History) Geology Series* **35**: 253–347.

Cruickshank, A.R.I. (1994). Cranial anatomy of the Lower Jurassic pliosaur *Rhomaleosaurus megacephalus* (Stutchbury) (Reptilia: Plesiosauria). *Philosophical Transactions of the Royal Society of London* B **343**, 247–260.

Cruickshank, A.R.I. (1996a). The cranial anatomy of *Rhomaleosaurus thorntoni* Andrews 1922. *Bulletin of the British Museum (Natural History)* Geology Series **52**: 109–114..

Cruickshank, A.R.I. (1996b). A *Pistosaurus*-like sauropterygian from the Rhaeto-Hettangian of England. *Mercian Geologist* **14**: .

Cruickshank, A.R.I. (1997). A Lower Cretaceous pliosauroid from South Africa. *Annals of the South African Museum* **94**: 196–226.

Cruickshank, A.R.I. and Fordyce, R.E. (in preparation). A plesiosaurian reptile from the Upper Cretaceous of South Island, New Zealand.

Dettmann, M.E., Molnar, R.E., Douglas, J.G., Burger, D., Fielding, C., Clifford, H.T., Francis, J., Jell, P., Rich, T., Wade, M., Rich, P.V., Pledge, N., Kemp, A. and Rozenfelds, A. (1992). Australian Cretaceous faunas and floras: biostratigraphic and biogeographic implications. *Cretaceous Research* **13**: 207–262.

Hocking, R.M., Moors, H.T., and van de Graaff, J.E. (1987). *Geology of the Carnarvon Basin Western Australia*. Bulletin **133**: xiv + 289. Appendices. Geological Survey of Western Australia, State Printing Division, Perth.

Long, J.A. (1993). *Dinosaurs of Australia, and other animals of the Triassic, Jurassic and Cretaceous Periods*. Reed Books, Sydney.

McLachlan, I.R and McMillan, I.K. (1976). Review and stratigraphic significance of southern Cape Mesozoic palaeontology. *Transactions of the Geological Society of South Africa* **79**: 197–212.

McLaughlin, S., Haig, D.W., Backhouse, J., Holmes, M.A., Ellis, G., Long, J.A. and McNamara, K.J. (1995). Oldest Cretaceous sequence, Giralia Anticline, Carnavon Basin, Western Australia: late Hauterivian-Barremian. *Journal of Australian Geology and Geophysics* **15**: 445–468.

McMillan, I.K. (in preparation). The Foraminifera of the Late Valanginain to Hauterivian (Early Cretaceous) Sundays River Formation of the Algoa Basin, Eastern Cape Province, South Africa. *Annals of the South African Museum*.

Massare, J.A. (1987). Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* **7**: 121–137.

Massare, J.A. (1988). Swimming capabilities of Mesozoic marine reptiles; implications for method of predation. *Paleobiology* **14**: 187–205.

Molnar, R.E. (1991). Fossil reptiles in Australia. In P. Vickers-Rich *et al.* (eds). *The Vertebrate Palaeontology of Australasia* 606–701. Pioneer Design Studios and Monash University Publications Committee, Melbourne.

Riess, J. and Frey, E. (1991). The evolution of underwater flight and the locomotion of plesiosaurs. In J.M.V. Rayner and R.J. Wootton (eds). *Biomechanics and Evolution*. Society of Experimental Biology Seminar Series **36:** 131–144, Cambridge University Press.

Schroeder, N. (in preparation). *A pliosaurid from the Early Cretaceous of Coober Pedy*. MSc Dissertation to be submitted to Monash University, Melbourne, Victoria.

Storrs, G.W. (1993). Function and phylogeny in sauropterygian (Diapsida) evolution. *American Journal of Science* **293** A: 63–90.

Tarlo, L.B.H. (1960). A review of the Upper Jurassic pliosaurs. *Bulletin of the British Museum (Natural History) Geology Series* **4**: 147–189.

Taylor, M.A. (1992). Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of the Yorkshire coast. *Philosophical Transactions of the Royal Society of London, ser.* **B, 335**: 247–280.

Taylor, M.A. and Cruickshank, A.R.I. (1993). Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia: Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire. *Philosophical Transactions of the Royal Society of London ser.* **B, 341**: 399–418.

Teichert, C. and Matheson, R.S. (1944). Upper Cretaceous ichthyosaurian and plesiosaurian remains from Western Australia. *Australian Journal of Science* **6**: 167–170.

Thurmond, J.T. (1968). A new polycotylid plesiosaur from the Lake Waco formation, (Cenomanian) of Texas. *Journal of Paleontology* **42:** 1289–1296.

Welles, S.P. (1962). A new species of elasmosaur from the Aptian of Colombia and a review of the Cretaceous plesiosaurs. *University of California Publications in Geological Science* **44**: 1–96.

Manuscript received 14 August 1996; accepted 3 December 1996.